HYBRIDISM IN THE GENUS VIOLA,— II.

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THE discussion of this subject, commenced over a year ago,[1] I purpose to resume in this and a subsequent paper. During the past year the problem has been studied persistently; most of the known aberrant forms of northeastern America have been grown in the garden; and several journeys through the coastal region of the Middle and New England States have been made to observe anomalous plants in their natural surroundings. I take pleasure in saying that in all this investigation I have been greatly assisted by the kindness of numerous students of the genus, who have sent me living plants and herbarium specimens, and have seemed to spare no pains to guide me to stations of special interest.

The result of these observations is to confirm in every particular the inferences of my previous article, and, furthermore, to bring to light some twenty-five additional hybrids and crosses in the genus Viola. In short, as regards at least the blue acaulescent violets of northeastern America the general rule seems to be inductively established, that *of the currently recognized species any two, that have been growing together for several years, are likely to present hybrids.*

Before entering upon the details of this evidence, certain preliminary matters should be presented, as helpful to a better understanding of the problem.

HYBRIDISM AMONG EUROPEAN VIOLETS.

It is interesting to note that in recent years a similar tendency to interbreed has been recognized in the European species of Viola. In the last edition of Garcke's Flora of Germany eighteen violet hybrids are reported as having been found among their twenty species. In a list of the plants of Norway and Sweden published in 1900 twenty-two violet hybrids are enumerated among their twenty-seven species. In a recent number of the Botanische Zeitschrift Dr. Heinrich Sabransky gives a list of ten species and nine hybrids that he has found in a

[1] RHODORA, vi. 213–223, NOV., 1904.

somewhat limited district of Austria, and remarks on the "most extraordinary tendency of the forms to hybridize; in no other genus does there appear such a multitude of hybrids as among the violets." Our blue stemless violets are all distinct from those of Europe, but the disposition to hybridize seems to manifest itself in all groups of the genus, and on both Continents.

Laws relating to known Hybrids among Flowering Plants.

To appreciate the evidence that certain forms of Viola are hybrids, one should have some definite knowledge of the usual behavior of known hybrids in other genera. This is well set forth in Focke's great work,[1] which contains a compendious account of the two or three thousand artificial and natural hybrids known at the time of publication, and discusses the general laws governing this group of phenomena. In regard to hybrids between *nearly related* but *distinct* species their behavior as a rule may be stated as follows:—

1. The hybrids have characters that are intermediate between the unlike characters of the parent forms.
2. They and their offspring are stable; that is, the several individuals resemble each other as closely as those that result from normal sexual reproduction.
3. They are more or less infertile, usually from defective pollen.
4. They are unusually vigorous in their vegetative functions; their flowers also are larger and remain longer in bloom.

These four laws precisely describe the behavior of the hybrids between any two *well-marked* species of our blue stemless violets. If one parent is pubescent and the other glabrous, the hybrid will be somewhat pubescent; if the cleistogamous peduncle in one is long and erect, and in the other short and deflexed, it will be of medium length and ascending in the hybrid; if the cleistogamous capsule is green in one parent and purple in the other, it will as a rule be green but more or less flecked with purple in the hybrid. Furthermore, the hybrids and their progeny are fairly constant. Thirty seedlings

[1] Die Pflanzen-Mischlinge von W. O. Focke, Berlin, 1881. Octavo, 570 pages; no English translation.

of *V. affinis*×*septentrionalis* have been under cultivation since July, 1904, and they all look just alike. About twenty plants of *V. cucullata* ×*fimbriatula*, from three different States show no appreciable difference. Also the infertility of these hybrids is most noticeable; rarely are more than 30 per cent of the ovules fertilized, usually about 10 per cent, occasionally none. Focke[1] has noted the marked infertility of the European hybrids of Viola. Lastly, the rank growth of violet hybrids is most pronounced. In many cases I have the hybrid growing side by side with the parent species, and always the robustness of the hybrid is strikingly apparent. I have frequently made eight or ten ample specimens out of one plant. On one individual of *V. affinis*×*sororia* I counted last May 148 large petaliferous flowers.

But when crosses are made between *doubtfully distinct* species, or between races, or between a species and its variety, there is commonly a marked departure from the first three of the laws above stated, viz.—

1. The offspring of such crosses have not intermediate characters, but various recombinations of the unlike characters of the parent forms.
2. The individual plants are consequently often dissimilar, some reverting to one or the other of the parent forms, others presenting all sorts of compromises,— a phenomenon known to breeders as "sporting."
3. There is no impairment of fertility either in the first or in subsequent generations.

To this class belong the so-called Mendelian hybrids,— the despair of the systematist, but the vantage ground of the breeder of new and useful "varieties."

The latest discussion of this subject is to be found in the recently published volume of DeVries. This author makes a sharp distinction between a specific and a varietal character. The latter he regards as but the loss or latency of a quality, which is positive and dominant in the typical form of the species. When interbreeding takes place, he holds that specific characters are affected according to the first set of rules above cited; but varietal characters according to the second set. I can make but the briefest allusion to this novel explanation of the phenomena of hybridism, and my excuse for so doing is that it seems to find illustration in the behavior of certain crosses between

[1] L. c., p. 477.

closely allied forms of Viola. DeVries holds that ordinary species "differ from each other partly in specific, partly in varietal characters. As to the first, they give in their hybrids stable peculiarities, while as to the latter, they split up according to Mendel's law."[1] This, as I hope to show, is exactly what takes place, when two such species as *V. fimbriatula* and *V. sagittata* interbreed. Dr. Sabransky also observes that in Austria "among the stemless violets, hybrids present for the most part a more or less distinctly intermediate character; while among the stemmed violets, they present an unbroken series of transitional forms between the parents, whose characters thus become confluent."[2]

Are specific Distinctions endangered by Hybridism?

Some systematists seem disturbed at the discovery that certain groups of nearly related species freely interbreed. It seems to admit, as one of our keenest observers has expressed it, the existence of "a mutually destructive influence, breaking down the individual characters of species, and merging them finally into one." Surely, hybridism is a movement in this direction. But we must remember that the advance of living organisms proceeds through the conflict of two opposing forces, the one leading to multiform variation, the other seeking to conserve the type by requiring double parentage. Thus the aberrant traits that may arise in an individual by mutation or fluctuation, are usually eliminated in succeeding generations by the repeated process of pairing with normal individuals. This conflict ordinarily ceases with the pronounced establishment of separate species; but within several groups of Viola, consisting of forms but recently ranked as species, the conflict seems to be exceptionally prolonged.

But we may, I fancy, discover the cause of this exceptional behavior. The power of sexual reproduction to maintain uniformity in a group of plants is so great, that for the evolution of two or more species out of one the incipient species need in some way to be isolated from each other. Darwin describes the fauna and flora of certain oceanic

[1] "Species and Varieties, their Origin by Mutation," p. 307.
[2] Translated from "Allgemeine Botanische Zeitschrift," xi. 162, Oct., 1905.

islands as consisting of species distinct from but allied to those of the neighboring mainland; free intercourse over a connecting isthmus would have largely prevented this divergence into two sets of species.[1] In many genera we know that certain species remain distinct only because each has its separate range; if through the agency of man they are brought together, they become more or less confluent through interbreeding.— Some years since I was interested in the study of Aquilegia; I got together as many species as possible of both the Old World and the New, and became quite familiar with the various types. Afterward, when they had been growing for several years without cultivation on the north side of an arbor-vitae hedge, my attention was attracted by the appearance of forms that I had never seen before. I found that at least five different hybrids had appeared spontaneously. Similar instances are by no means rare.

An analogous cause has disturbed the relations to each other of our species of common blue violets. Two or three centuries ago the north-eastern United States was entirely covered with forests. The clearing away of these forests by man has profoundly modified the conditions of plant life. With the exception of *V. palmata*, our blue stemless violets are rarely found, and certainly do not thrive, in the primeval forest; they are rather plants of open groves, of fence-rows, and moist meadows. When the whole country was densely wooded, their growth must have been greatly restricted; but when the trees were removed they had a chance to 'run and be glorified'; their range was vastly extended; the number of individuals increased perhaps a thousand-fold; species before isolated became cohabitant, and had opportunities to hybridize.[2]

How far this movement of involution will extend, it is idle to speculate. But so far as regards the survival of our species of Viola we need give ourselves no concern; for the vast majority of its seeds are produced from the self-fertilized flowers, and must therefore be free from admixture with other species. However readily the petaliferous flowers may produce hybrids, these hybrids must always be greatly outnumbered by the legitimate offspring.

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[1] The Origin of Species, 6th ed., ii. 177–182.

[2] It would be interesting to follow out this line of thought in its bearing on other groups of species, such as Crataegus and Rubus. There are not wanting grounds for the suspicion that they too, since the forests were cleared, have enormously multiplied, and have been behaving badly,—producing hybrids and Mendelian crosses,— sporting wantonly, — at the expense of the makers of species.